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A HOLLOW SPINED *ANAPACHYDISCUS PENINSULARIS*
WITH POSSIBLE MOSASAUR BITE IMPRESSIONS

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A HOLLOW SPINED *ANAPACHYDISCUS PENINSULARIS* WITH POSSIBLE MOSASAUR BITE IMPRESSIONS¹

By LouElla R. Saul²

ABSTRACT: A specimen of Early Maestrichtian age *Anapachydiscus peninsularis* (Anderson and Hanna) from Arroyo Santa Catarina, Baja California, Mexico, has nearly round holes punched in the shell so arranged that they suggest mosasaur bite marks. The early whorls are ornamented with hollow lateral spines which could have served as vertical stabilizers.

A concretion of roughly 20 cm diameter protruding from the near vertical side of a gully cut into Rosario Formation siltstone was overlooked by local entrepreneurs who, in 1968, collected for use in the manufacture of lamp bases, etc., all exposed or near surface ammonites from the well-known locality in Arroyo Santa Catarina, Baja California, Mexico. A blow or two with sledge and chisel split the concretion and freed from the rock a well-preserved ammonite, *Anapachydiscus peninsularis* (Anderson and Hanna). Matrix plugs remained in the umbilicus, and a lump of siltstone adhered to and filled what remained of the broken body chamber. Four curiously round holes, two on each side marred the specimen. Their shape, spacing and alignment are reminiscent of those in the mosasaur-bitten ammonite described by Kauffman and Kesling (1960). The siltstone matrix at the apertural end was sawed away and most of the plug in the umbilicus on the right side was removed so that the specimen might be used to display evidence of interaction between animals. Removal of the matrix in the umbilicus exposed one more roundish hole in the shell and, bordering the umbilicus, hollow spines which have not been previously noted in descriptions of this species (Anderson and Hanna 1935, p. 20, pl. 4, fig. 1; pl. 5, fig. 1-2; pl. 6, fig. 3-4; pl. 7, fig. 5; text-fig. 1; Anderson, 1958, p. 225; Matsumoto, 1959, p. 38).

THE ROUND HOLES

The holes are not truly round, but give the impression of having been punched by round objects intersecting the curved, ribbed surface of the ammonite shell. In addition to the five roundish holes — two on one side, three on the other — the specimen has a small angular hole (Fig. 6) on the abapertural side of the umbilicus that could have been made by the tip of a tooth. The shell is not depressed around the holes as in the specimen described by Kauffman and Kesling (1960), but each hole has cracks radiating from it. The holes are in the chambered portion of the conch, and the edge of the shell along which most of the body chamber broke off resembles a tear along perforations. If the rounded embayments of this edge are considered to represent half-tooth marks, there are ten tooth marks. Figures 1 and 2 diagram two possible bites. The plump rounded whorls of *A. peninsularis* are not as advantageously shaped for displaying the bite of a mosasaur as is the discoidal shape of the *Placenticer* of

Kauffman and Kesling (1960), and other sortings of the holes into bites can be argued for. Camp (1942) discussed two genera of mosasaurs from the Maestrichtian of California, *Plotosaurus* and *Pleisiotylosaurus*, but the limited record of these "bites" (Figs. 1-3, 5-6) does not indict either. This probable mosasaur may have regularly dined on ammonite as it seems to have been more efficient about acquiring the benefits of its chase than did the one inferred by Kauffman and Kesling. The Baja California mosasaur apparently required only two bites to break off the body chamber and thus free the edible soft parts rather than the 16 bites shown on the *Placenticer*. An even more adept mosasaur might bite just at the rear of the body chamber and leave as a record of its predation only the torn-on-perforations shell edge.

THE HOLLOW SPINES

The spines on the specimen, UCLA cat. no. 38765, are formed by a thin outer layer of the shell (3rd abapertural spine of figure 5 has wall .3mm thick) and are readily removed along with the matrix leaving as their bases of attachment, bordering the umbilicus, the flat-topped tubercles of previous descriptions (Anderson and Hanna 1935, p. 20; Anderson 1958, p. 225). The maximum diameter of this specimen is 11.8 cm; the last flat-topped tubercles occur at a diameter of about 7.3 cm. The spines and spine bases have been best exposed on the last whorl of their occurrence; here they are not evenly spaced; they occur on every second to fourth rib. They appear to be more regularly spaced on earlier whorls. The tallest spine (incomplete) is 8 mm high; it is the next to the last abapertural one preserved (figure 5) and is filled with crystalline calcite. The last spine is 6.5 mm high, has the tip closed, and is probably nearly complete. The outermost end of all the earlier formed ones were damaged in preparation,

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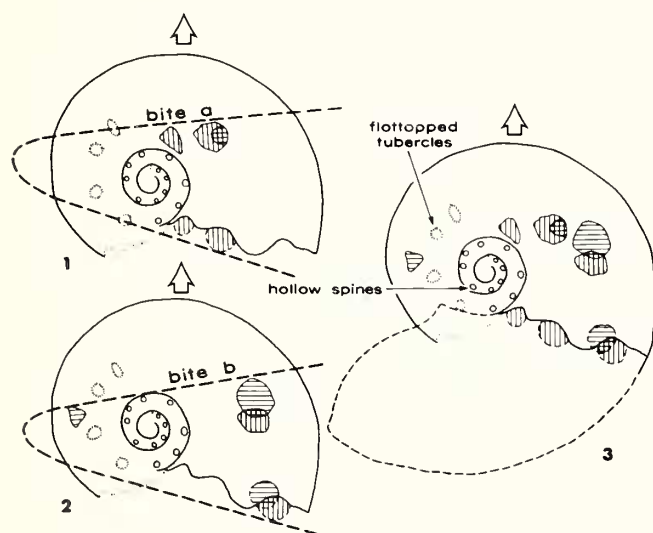
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TABLE 1
Measurements (in mm.) of *Anapachydiscus peninsularis* (Anderson and Hanna.)

cat. no.	maximum D	maximum W	last flat-topped tubercle W D	W/D	
CAS 4250	41.5	27.5	too poorly preserved	.66	paratype, poorly preserved
CAS 4253	92	55	36 (60)	.6	paratype
UCLA 28717	107	58	29.5 (54)	.54	hypotype
UCLA 38765	118	67.5	51 (89)	.57	hypotype, with spines and holes
CAS 4249	120	64	42 (79)	.53	paratype, one spine showing?
CAS 4257	123	72	50 (85)	.58	paratype
CAS 4248	355	144	too poorly preserved	.41	holotype

D = diameter; (D) = diameter calculated from width of whorl; W = width of whorl; CAS = California Academy of Sciences; UCLA = University of California, Los Angeles. The average diameter at which *A. peninsularis* apparently ceased to generate spines was 73 mm.; however, two specimens, 4253 and 28717, ceased notably sooner at an average diameter of 57 mm. than the other three measurable specimens which ceased at an average of 84 mm. The gap in estimated size at which they ceased to grow spines may result from measuring too few specimens or it may be an indication of sexual dimorphism. The ratio W/D shows a loss of inflation with increase in size.

some because these structures were unexpected and the others because they are so frail that they adhered to the matrix being removed. All except the two abapertural spines are filled with siltstone and thus were broken prior to entombment. Earlier formed spines appear to have been longer relative to the size of the ammonite shell than the later ones. The thin-walled, hollow spines were sealed off at their bases by the formation of the next



FIGURES 1-3. *Anapachydiscus peninsularis* (Anderson and Hanna) with aligned rounded holes. Holes of near side vertically lined, of far side horizontally lined. Ammonite in presumed living position, arrows point up. Because of the size of the ammonite and its inflation, too few "tooth marks" are present to determine direction of bite, but two bites seem to be required by the positions of the holes. Figures 1 and 2 diagram two of several possible positions for the bites. Figure 1. Bite *a* caught the ammonite and began to break off the body chamber. Figure 2. Bite *b* broke off the body chamber. Figure 3. All holes indicated and body chamber restored. Inferred body chamber length from Raup (1967, text-fig. 16) is minimum length and results in most horizontal bite. A longer body chamber rotates the diagrammed ammonite counter-clockwise and suggests attack from above.

inner shell layer. The umbilical wall of the enveloping whorl does not touch the spines; there is now a thin layer of siltstone between spine and umbilical wall, and the spines apparently stood free.

The original type lot of *Parapachydiscus peninsularis* Anderson and Hanna comprises five specimens. Of these, three are not well enough preserved to show spines or flat-topped tubercles. The smallest specimen, California Academy of Sciences cat. no. 4250, has strong ribs with obvious tubercles bordering the umbilicus; but if the tubercles had rimmed flat-tops, weathering has obliterated this detail. The specimen is, however, because of the strength of the ribs, listed in Table 1 as having been spiny throughout. With spines of equivalent length to those on UCLA cat. no. 38765, it would have had a ventral profile like that in figure 4. One of the paratypes, CAS cat. no. 4249, has a circlet of shell that is probably a spine showing through the matrix in the umbilicus. As can be seen from Table 1, the size at which *A. peninsularis* ceased to grow spines was not consistent. UCLA cat. no. 28717 (Popenoe 1954, fig. 3 (9)) had a width of only 29.5 mm when its last spine formed; but UCLA cat. no. 38765 has its last flat-topped tubercle at a width of 51 mm. The difference between the two specimens of least diameter and the three of larger diameter may reflect sexual dimorphism, but the sample is too small to be significant.

An *Anapachydiscus* was collected by John Alderson from the NW¼ of section 6, T24S, R16E, Cholame 7½ min. quad., Monterey Co., California (UCLA loc. 6337), or approximately 1 mile westward along strike from LSJU (Stanford University) loc. 3354, from which Matsumoto (1959, p. 38; 1960, p. 127) identified *Anapachydiscus* cf. *A. arrialoorensis* (Stoliczka). Alderson's specimen (UCLA cat. no. 57245) is plumper and has closer spaced stronger ribs than specimens of *A. peninsularis* from Baja California, and thus resembles Stoliczka's (1865, p. 126, pl. 63, fig. 2-4; pl. 64, fig. 1) figures of *Ammonites arrialoorensis*. It differs from these figures in having more elliptical spine bases.

The outer whorl(s?) of Alderson's Cholame specimen was broken and eroded and discarded in the field leaving a specimen, septate throughout, with diameter 90.5 mm and width 53 mm. Most of one volution is present, the inner whorls being broken. A flange of shell that formed the umbilical flank of the next outer

volution remains on the right side of the specimen. The thickness of this umbilical flank shell is about .6 mm. Broken hollow spines are present at a diameter of 68 mm, width approximately 33 mm. The spine wall is almost one-third the thickness of the flank wall. Spines appear to have been formed at a diameter of 87 mm, width 49 mm, but preservation and breakage are such that I cannot be sure of their presence or absence. Also the spines are less obvious than on UCLA cat. no. 38765 because in the Cholame specimen the enveloping umbilical wall nearly engulfs them. Considering the size to which some *Anapachydiscus* grew, they seem to have had remarkably thin shells. Their shell walls were about one-half as thick as those of *Nautilus pompilius* and only a third thicker than that of an argonaut of similar diameter.

The spines were apparently secreted at the apertural edge as part of the outermost layer of the conch. There is no evidence that the leading side of the spine was open as is commonly the case with spines arming the aperture of a gastropod. Compared to spines on *Murex* spp., the spines on *Anapachydiscus* have a wall that is one-half to one-third as thick and is of equal thickness all around. The diameter of the hollow center is approximately 3 times the thickness of the spine wall. Spines on *Murex* spp. have adaperturally placed holes whose diameters are one-third or less the thickness of the spine wall. The sealing off of the bases of the *Anapachydiscus* spines probably took place soon after their formation as the next inner strengthening layer of the conch was deposited. Since the spines were apparently not open along their leading edge and were probably soon sealed off at their base, it seems unlikely that they functioned as supports for soft parts at the aperture edge or as channels for current flow.

Teichert (1967, p. 204) included spines on ammonites in his tabulation of adaptive devices to regulate buoyancy. Kennedy and Cobban (1976, p. 28) suggested that spines might serve as balancing aids when the shell rested on the bottom or as horizontal stabilizers to prevent yawing. Westermann (1971, p. 7) has listed as functions of ornament on ammonites: strengthening the relatively thin shell against implosion, protection against impact, protection against smaller predators, decrease of drag under conditions of turbulent flow, and camouflage. Arkell, Kummel, and Wright (*in* Moore 1957, p. L122) suggested that spines could have served as balancers or stabilizers or as a protection against enemies. It is this latter function that Westermann inferred lateral and ventrolateral spines to have served. Cephalo-

pods of all kinds are noted for their varied camouflage techniques (Lane 1960, p. 93–104; Cowen et al. 1973; Young and Roper 1976), and Cowen et al. (1973) suggest that the primary function of ammonite ornament was camouflage for a nekto-benthonic organism.

Ornament to decrease drag is more likely to be ribbing or nodding than long spines (Chamberlain and Westermann 1976, p. 329). Such long frail spines were probably not secreted to strengthen the shell. They could have offered some protection against impact, absorbing some of the impact energy or perhaps more importantly putting distance between the primary impact

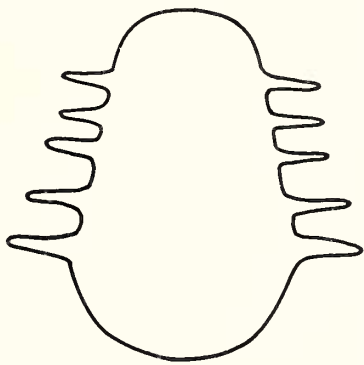


FIGURE 4. Reconstruction of ventral view of young *A. peninsularis*. Ammonite outline based on CAS 4250 and spines similar in length to those on UCLA 38765 added. Spines produce an obviously unstreamlined outline and effectively increase width of ammonite with respect to height.



FIGURES 5–6. *Anapachydiscus peninsularis* (Anderson and Hanna). UCLA hypotype cat. no. 38765, $\times 3/4$. (5) lateral view with three rounded holes and "torn-on-perforation" edge to broken body chamber. Twelve hollow spines show in umbilicus and are followed adaperturally by four flat-topped, rimmed tubercles. (6) opposite side of figure 5 with two rounded holes and on opposite side of umbilicus one triangular hole interpreted as being made by tip of tooth. Six flat-topped, rimmed tubercles bordering the umbilicus considered to be bases of hollow spines.

and the conch, but if this were their main function a more useful placement would seem to be nearer the unprotected venter, especially if the ammonite was nekto-benthonic. Nor do they seem well placed as defensive armaments. Gastropods arm their aperture and anterior siphon; the bivalve *Hysteroconcha* has spines on its corcelet which thus surround the siphons; but the spines on young *Anapachydiscus* neither surround soft parts nor are they on the outer perimeter of the animal to discourage attack. They are thinner walled and even though liquid filled were apparently frailer structures than the probably defensive spines of the gastropods and bivalves. They would have increased the apparent size of the young ammonite and so might have discouraged some smaller predator. The need for camouflage (Cowen et al. 1973, p. 211) was in part inferred from the paucity of ammonite specimens showing pigmentation, but some few specimens have been found (e.g., Arkell in Moore 1957, p. L92; Reymont 1958) and some indicate the presence of *Nautilus*-like counter shading.

Surrogate ammonites were formed of sculpturing and investing waxes. The investing wax was heavier, the sculpturing wax lighter than water. As it has been suggested that ammonite and shell were of near neutral buoyancy (Trueman 1941; Raup and Chamberlain 1967), waxes were melted together empirically until disks of approximately neutral buoyancy were obtained. These disks were of similar diameter and width to the small paratype CAS cat. no. 4250. Being homogeneous, they lacked the orienting separated centers of gravity and buoyancy of actual ammonites (Trueman 1941, figs. 14 and 15). Such a wax disk, lighter than water, comes to rest floating with either lateral side up and the venter directed horizontally. Disks of near neutral buoyancy also usually settled toward a similar position, and a heavier disk sank and usually lay flat on the bottom. The addition of lateral spines gave the disks vertical stability, and they floated or sank with the venter directed vertically. For the light disk the spines had to be quite long to change its orientation in the water, at least twice as long as those on *A. peninsularis*. Spines of similar length to those on *A. peninsularis* gave the neutrally buoyant and heavier disks vertical stability and greatly slowed the descent of the heavier disk. Vertical stability could also be achieved by carving out rough umbilici and adding the wax to the ventrolateral margin to produce a shape similar to young *Tropites subbullatus* (Hauer). The greater breadth of young *A. peninsularis* relative to adult (Table 1) may have also tended to increase vertical stability in the young although the breadth of young *A. peninsularis* is not great enough to produce vertical stability in the absence of spines. Spines are not considered to have provided all vertical stabilization. Well separated centers of buoyancy and gravity would also lend vertical stability in addition to apertural stability, but the somewhat depressed form and probably longer body chamber (Raup 1967, fig. 16) of young *A. peninsularis* would have caused the centers of buoyancy and gravity to be closer together (Trueman 1941, p. 371). The spines would have provided added stability. They were of appropriate length to provide a neutrally buoyant ammonite similar to the small paratype with vertical stability.

A pelagic youth has generally been assumed for ammonoids (Arkell, Kummel, and Wright, in Moore 1957, p. L100; Kennedy and Cobban 1976, p. 34). Cowen et al. (1973, p. 211) suggest that the sculpture of ribbed ammonites indicates that they were nekto-benthonic inhabitants of the photic zone, their sculpture serving to hide them from the predator above, and their close association with the bottom insuring that there was seldom a

predator below. That ammonites lived in the photic zone is also suggested by the discovery that unlike the nocturnal *Nautilus* and some deep water octopods, at least some ammonites had an ink-sack (Lehmann 1971a, p. 1262). As the spines on young *A. peninsularis* and *A. cf. A. arrialoorensis* would not have improved the streamlining of a shell which was already poorly streamlined (Kummel and Lloyd 1955; Chamberlain 1976), swimming must have been at a rather deliberate pace, the entrapment of food effected without much darting about. The holotype of *A. peninsularis* is over 35 cm in diameter and much less strongly ornamented on its outer whorls and similarly less ornamented than specimens of less than 9 cm diameter. This reduction in relief of ribbing can be considered to accord with findings of Chamberlain and Westermann (1976, p. 328) that ribbing can serve to reduce drag and conserve propulsive power on smaller ammonites, but that large ones should be smooth. Young *A. peninsularis*, however, additionally had spines, and it does not merely become smoother as it approaches 10 cm in diameter; it also becomes higher relative to width and reduces the relative size of its umbilicus, thus improving streamlining slightly.

This complex of morphologic changes suggests that spiny young *Anapachydiscus peninsularis* may have been virtually planktonic and feeding on plankton. Ammonites have usually been considered to share the macrophagous diet of other living cephalopods, but a microphagous plankton-feeding mode of life has been suggested for some (Morton and Yonge in Wilbur and Yonge 1964, p. 49; Busnardo 1965, p. 110; Kennedy and Cobban 1976, p. 35), and Lehmann (1971b, p. 339) reports the preserved crops of ammonites containing the remains of prey too

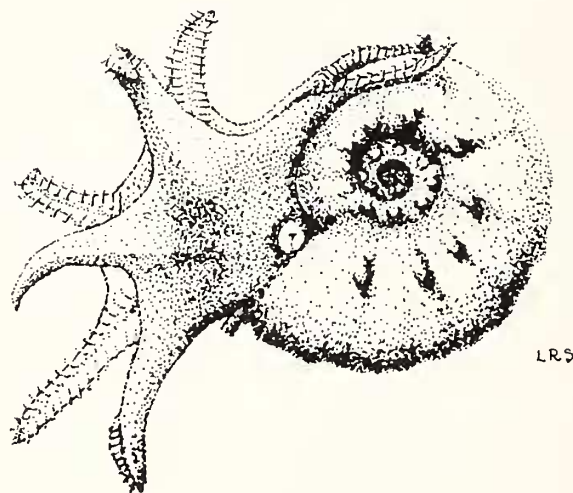


FIGURE 7. Hypothetical ammonite with eight webbed cirrated arms. Webbed arms suggested by distribution of epizoans of Seilacher (1960) and Meischner (1968). In both cases the epizoans were able to settle on the living ammonite shell posterior to the aperture and on the body chamber especially on the venter. They did not settle on the conch above the aperture. If the ammonite had tentacles as does *Nautilus* this selective infestation would not be expected, and long arms as in *Argonauta* would be able to sweep the whole conch clean. But webbed arms should be able to remove any larvae from the conch above the aperture while being restrained from reaching the lower and rearward portions of the conch. Webbed arms could be used to trap food or also for propulsion as in octopods (Lane 1960, p. 69).

small for the application of jaws. Studies of the jaws themselves (Kaiser and Lehmann 1971) indicate that the jaws of ammonites were not capable of actual biting. Reconstruction of the living ammonite is often based on analogy with *Nautilus* (e.g., Arkell in Moore 1957, p. L82, fig. 124); but *Nautilus* may be a poor model for ammonites (Mutvei and Reymont 1973; Kennedy and Cobban 1976, p. 2). Lehmann (1971a and b) has shown that the radula of ammonites is more like that of octopods and Vampyromorpha; and Flower (1955, p. 866) has argued for fewer arms, than the 60+ tentacles possessed by *Nautilus*, in groups considered ancestral to ammonites (Sweet and Moore in Moore 1964, p. K101, fig. 70). Mutvei and Reymont (1973, p. 632) propose a long bodied ammonite without funnel. But their proposed long ctenidia in narrow mantle cavity would require maintenance of a current of water to ward off asphyxiation, and as the funnel is primarily a means of ejecting from the mantle cavity water which has passed over the ctenidia, the funnel is here retained to aid respiration. Figure 7 equips young *A. peninsularis* with eight webbed cirri-bearing arms. The position of the arms back over the upper part of the shell was suggested by the distribution of epibionts described by Seilacher (1960) and Meischner (1968). Webbed arms with cirri (as suggested by Kaiser and Lehmann 1971, p. 31) could have been used by young planktonic *A. peninsularis* to gather in a planktonic feast as its outrigger spines steadied it in the water.

The abandonment of spines, reduction of sculpture, increase of height and decrease of umbilical size may mark the change to greater swimming ability and more actively pelagic life. The thinness of the shell suggests that this did not lead to the exploration of great depths.

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RESUMEN

Un espécimen de la temprana época Maestrichtian *Anapachydiscus peninsularis* (Anderson y Hanna) de Arroyo Santa Catarina, Baja California, México, tiene cavidades casi redondas taladradas en la concha arregladas de tal manera que sugieren muestras de las mordeduras del mosasaur. Las tempranas espirales están adornadas con huecas espinas laterales, las cuales podrían haber servido de estabilizadores verticales.

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